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Differential mortality of wintering shorebirds on the Banc d'Arguin, Mauritania, due to predation by large falcons

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Predators may influence many aspects of the daily life and seasonal movements of their prey. Here we quantify direct, and evaluate indirect effects of predation by three falcon species (Lanner Falcon *Falco biarmicus*, Barbary Falcon *Falco pelegrinoides* and Peregrine Falcon *Falco peregrinus*) on coastal shorebirds wintering on the Banc d'Arguin, Mauritania, an area hosting approximately 30% of the East Atlantic Flyway population of shorebirds. On the basis of 754 h of observation over five winters, 97 witnessed attacks and 585 collected prey remains, we show that shorebirds were safer in larger flocks, which tended to be attacked less often. Furthermore, species that forage relatively close to shore and in small flocks were depredated more often than expected from their relative abundance. In three species, Red Knot *Calidris canutus canutus*, Bar-tailed Godwit *Limosa lapponica taymyrensis* and Dunlin *Calidris alpina*, the juveniles were more vulnerable than adults. We estimated that on average 1% of the juvenile and 0.1% of the adult Red Knots present were killed by large falcons each winter. For Red Knots we simultaneously quantified annual survival on the basis of an individual colour-marking programme: mortality due to predation by falcons accounted for an estimated 6.2% (juveniles) and 0.8% (adults) of annual mortality. We suggest that juvenile Red Knots are 10 times as likely to be killed by falcons because they use riskier habitats, i.e. early and late tide foraging areas closer to shores where surprise attacks are both more common and more successful. These results indicate that the strength of indirect effects of predation operating in a shorebird population largely outweigh the effects of mortality *per se*.

Keywords: age-dependence, annual survival, falcons, habitat selection, mortality, non-lethal effects, predation, Red Knot.

Coastal shorebirds have much to fear from fast aerial predators, especially falcons (Dekker 1980, 1988, 2003, Bijlsma 1990, Buchanan 1996, Fuller *et al.* 1998, McGrady *et al.* 2002, Ydenberg *et al.* 2004). Even if predators kill few animals relative to the total population, these predators may have non-lethal, indirect effects on bird numbers and distributions via behavioural decisions of the prey, which could far outweigh the lethal effects (Newton 1998, Lind & Cresswell 2005). For instance, differences in death rates between classes of individuals (i.e. species or age-classes) could result from differences in the ways that they trade-off starvation and predation (e.g. Lima & Dill 1990). Therefore, mortality *per se* is not the relevant measure of total predation impact (Lank & Ydenberg 2003, Lind & Cresswell 2005, Ydenberg *et al.* 2007). Such indirect effects have been claimed in a number of studies on various invertebrate and vertebrate animal species (Sih *et al.* 1985, Anholt & Werner 1995, Nakaoka 2000, Creel *et al.* 2007, Heithaus *et al.* 2007).

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For several coastal sites it has been documented that avian predators kill a sizeable part (up to half) of the available shorebirds over single winter periods (Page & Whitacre 1975, Whitfield 1985, Cresswell & Whitfield 1994). However, it is quite possible that atypical sites with high raptor attack rates have attracted students of raptor predation. To put predation by raptors in proper demographic and evolutionary contexts (e.g. see Lima & Dill 1990, Lank *et al.* 2003, Ydenberg *et al.* 2004), we need estimates of mortality rates from major wintering sites, i.e. sites selected on the basis of their importance for shorebirds, rather than for the ease of witnessing raptor predation.

With two million wintering shorebirds, about one-third of the entire East Atlantic Flyway population (Altenburg *et al.* 1982, Smit & Piersma 1989, Zwarts *et al.* 1998, Davidson & Stroud 2006), the Banc d'Arguin in Mauritania clearly qualifies as a site of major importance. Building on a major research effort to quantify annual survival and site-faithfulness in Red Knots C*alidris canutus canutus* (e.g. Leyrer *et al.* 2006), we have embarked on a study of the impact of predation by raptors relative to overall rates of mortality. We here present the full dataset accumulated over five consecutive winters on rates of attack, attack success and prey selection by aerial predators.

STUDY AREA AND METHODS

Study area

The Banc d'Arguin is an area of shallow water and islands that stretches along the northern coast of Mauritania, bordering the Sahara desert from about 20°50′N, 16°45′W to 19°20′N, 16°28′W. Part of this area, including 500 km^2 of intertidal flats, is protected as a national park. The Parc National du Banc d'Arguin covers a total of 12 000 km^2, 6300 km^2 of which is open shallow seas (Altenburg *et al.* 1982, Wolff & Smit 1990, Isenmann 2006).

The fieldwork was carried out on and around the Iwik peninsula (19°53′N, 16°17′W, Fig. 1), named after the fishing village of Iwik (around 200 inhabitants), an area which we assume to be representative for the entire Banc d'Arguin. Of a total area of 50 km^2, approximately 22 km^2 is occupied by tidal mudflats, which are largely covered by seagrass (*Zostera* spp.), salt plains (sebkha) and desert. Two shallow bays are located on either side of the peninsula. Northwest of Iwik is Ebelk Aiznay and northeast of the village lies a much larger bay, the Baie d'Aouatif (Fig. 1). At Ebelk Aiznay and along the eastern part of the peninsula

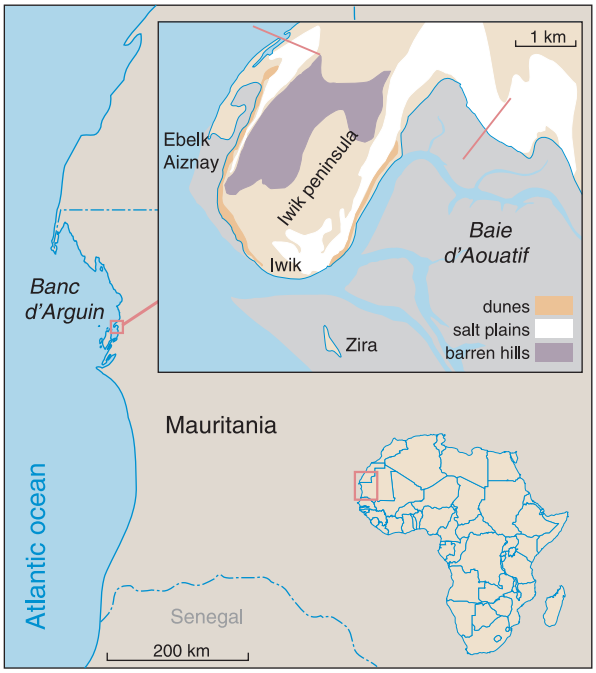

Figure 1. Map of the study area. Records of raptor attacks are confined to the coastal zone of the Iwik peninsula between the red strokes north of Ebelk Aiznay and in the Baie d'Aouatif. The central purple area are the barren hills where large falcons usually rest and from where they launch the majority of their attacks. The sebkha (salt plains) are depicted in white, whereas the dunes that border the mudflat are shown in orange.

Figure 2. The landscape on the Iwik peninsula: the barren hills on the left provide resting places for the falcons. The dunes bordering the mudflats are used by the falcons to launch stealth attacks (photo by F. Robin).

the mudflats are separated from the sebkha by low dunes covered with a sparse vegetation of succulents (Fig. 2). The central part of the peninsula consists of low barren hills (not higher than around 15 m).

Table 1. Study period, high tide counts, observation effort and large falcon species present in the study area

				Lanner		Barbary		Peregrine	
Year	Period	High tide counts	Observation hours	♀	♂	♀	♂	♀	♂
2002	24 Nov.–11 Dec.	6 Dec.	143	1	1	1	1		
2003	11–29 Dec.	26 Dec.	119			1	1		
2004	28 Nov.–17 Dec.	17 Dec.	66	1	1	1	1		
2005	16 Nov.–8 Dec.	8 Dec.	196	1	1	1		1	1
2006	7–27 Dec.	16 Dec.	230	1	1	2			

Raptor observations

This study was carried out from 2002 to 2006, with five consecutive winter visits of several weeks. A total of 754 h were spent on raptor observations, of which approximately 75% were 'systematic' observations, i.e. observations that were not combined with other activities such as shorebird foraging studies or searching for colour-marked birds.

Large falcons were identified to species, and sex and age if possible. Three species, Lanner Falcon *Falco biarmicus*, Barbary Falcon *Falco pelegrinoides* and Peregerine Falcon *Falco peregrinus*, were encountered. Records were kept of their hunting efforts with respect to location and tidal cycle (see Dekker & Ydenberg 2004). Furthermore, hunting method, flock size attacked and the result of the attack (success or failure) were recorded. Hunting methods included low-level surprise attacks, open attacks, stoops from soaring position and co-operative hunting (Dekker 1980, Bijlsma 1990). In line with most studies, an attack was considered as an attempt to seize or knock down an individual prey during a hunting flight (Kus *et al.* 1984, Buchanan *et al.* 1988). When a raptor changed target, for example after a shorebird flock had broken up into smaller units, we recorded this as multiple capture attempts (Page & Whitacre 1975). When a bird was captured, this was considered a successful attack.

The hills of the central part of the peninsula (Figs 1 & 2) were favourite perches for the falcons and were points of departure for attack flights. All but one of 97 observed hunting flights (in 575 h of observation time) took place on the peninsula. Attack rate and mortality due to predation were calculated with respect to the coastal area around the Iwik peninsula only (Fig. 1). This should cover most if not all predation events in the general study area as no falcon hunts were recorded on the outer mudflats during 22 h of observation (see Fig. 1). The area east of the red line in Figure 1 was not included because only 27 h of observations were spent there.

Prey remains

During all field periods we systematically searched the coastline for prey remains, which were collected and identified to species. Red Knot, Dunlin *Calidris alpina* and Bar-tailed Godwit *Limosa lapponica taymyrensis* were identified as adults or juveniles following Prater *et al.* (1977). Jackals *Canis aureus* scavenged for dead and dying prey and their prey handling could be easily distinguished from that of large falcons, as Jackals bite off feathers, whereas falcons pull out feathers one by one and leave the wings, sternum and girdle largely intact (Bijlsma 1990).

Bird counts

Once in each of the winter periods, simultaneous high-tide shorebird censuses, by 8–10 people, were executed (Table 1). In 2002–03 no counts were available for the island of Zira (see Fig. 1), and thus for estimates of direct mortalities we used counts from 2004–06 only.

During 13–23 December 2006 at Ebelk Aiznay, bird numbers were counted over four tidal cycles in a quadrant of 100 × 75 m on eelgrass (N. Spaans pers. obs.), which gave us a picture of forager abundance until habitat became unavailable due to high tide. Throughout the studies, we made notes on differences in shorebird habitat use, such as distance from cover. This was done separately by species and, for Red Knot in particular, by age-class. Detailed mechanisms concerning age-related habitat use in Red Knots will be reported elsewhere (P.J. van den Hout unpubl. data). Following methods in Piersma *et al.* (1993) for Red Knot at Ebelk Aiznay, in December 2006 P. de Goeij recorded the frequency distribution of the size of Red Knot flocks encountered.

Mist-net trapping and survival analyses

Each winter we trapped shorebirds with mist-nets during the calm nights around the new moon with the highest water levels (B. Spaans unpubl. data). This enabled us to determine body masses (which we used for raptor requirement calculations) and age-proportions (particularly for Red Knot, Dunlin and Bar-tailed Godwit) and to mark Red Knots as part of demographic studies. A detailed study in Scotland showed no evidence that colour-ringing affected predation mortality (Cresswell *et al.* 2007).

The Red Knots that we caught with mist-nets were individually colour-marked. On the basis of resightings of these marked individuals (Leyrer *et al.* 2006) using the standard Cormack–Jolly–Seber method in the software program MARK (White & Burnham 1999), we calculated annual (from summer to summer) survival rate. Removing the effects of transients in the estimate of the first year after capture (Sandercock 2003) for adults, the estimated survival 2 years and more after the year of capture was considered to be the best estimate. The transient-effect is reflected by the low value of Φ_2 shown in Table 3; it was considered to be absent for juveniles which remain on the Banc d'Arguin in their first 2 years of life (Piersma *et al.* 1992). Estimates were based on the resighting of 992 individually marked Red Knots. Of these, 244 (193 adult, 51 juvenile) were ringed in 2002, 196 (133 ad., 63 juv.) in 2003, 201 (133 ad., 68 juv.) in 2004 and 161 (139 ad., 22 juv.) in 2005. Because all Red Knots in this sample were ringed on the Banc d'Arguin in November–December, mortality either by starvation, disease or predation of juvenile birds on their first journey from the breeding to the wintering grounds is not included in this analysis.

Calculation of predation rates

Predation rates (kills/h) were calculated by multiplying falcon success (no. kills/no. attacks) from attacks with known outcome by the total number of attacks observed per hour of observation. Because it was often impossible to identify the shorebird species that were attacked, to calculate predation rates for each species we multiplied the overall predation rate by the collective abundance of each species identified in the prey remains that we collected. To estimate the relative mortality ('vulnerability index') of each shorebird species, we subtracted the proportion ($\log_{10}$-transformed) of each shorebird species based on the data collected from species counts at high tide ('expected') from the proportion ($\log_{10}$-transformed) of each species found in the prey remains ('observed'; see Møller & Nielsen 2007). A value of 0.5 indicates that a species was five times more likely to be killed by a falcon than expected based on its relative abundance. We use the term 'vulnerability' as a synonym of this likelihood (predation risk). Vulnerability is affected by a number of factors such as habitat selection, feeding behaviour and flock size (Lank & Ydenberg 2003).

In similar manner, but for each species separately, by comparing the fraction of juveniles as found in the prey remains to the fraction of that age-class among birds caught with mist-nets, we calculated relative mortalities for juveniles in Dunlin, Red Knot and Bar-tailed Godwit. We assumed that our mist-net catching gave an unbiased estimate of age composition although we realize that this is not always and not necessarily the case, especially during small catches at marginal locations and times (Pienkowski & Dick 1976, Clark *et al.* 2004, McCaffery *et al.* 2006). Currently, we have no way to assess the magnitude of any such bias. For species and age-classes, χ^2 tests for goodness of fit were applied to test whether observed prey significantly differed from expectation. When only two groups were compared, as in age-class comparisons, a Yates' correction for continuity was applied (Zar 1999).

For each shorebird species we determined the percentage of annual mortality that could be accounted for by predation. We tallied the number of individuals killed by predators per species throughout the study period (2002–06) and calculated the average number of individuals killed per 7-month overwintering period (Page & Whitacre 1975). These averages were divided by the local number of each species as determined by the high tide shorebird censuses (Table 1).

We examined the robustness of the overwintering mortality estimates by comparing total bird mass (including waste) depredated with the estimated requirements of falcons (Whitfield 1985, Whitfield *et al.* 1988). Total bird mass taken by raptors was estimated by expressing the species killed by raptors in body mass equivalents (body mass was derived from mist-net catches). Food requirements of falcons were based on estimates for adult Peregrine Falcons and linearly adjusted to other falcon species according to the raptors' body mass (Cramp & Simmons 1980, Ratcliffe 1993). For temperate climatic conditions we calculated that the food (including waste) needed per day varied from 11.5% of body mass in summer to 15% in autumn for a male Peregrine,

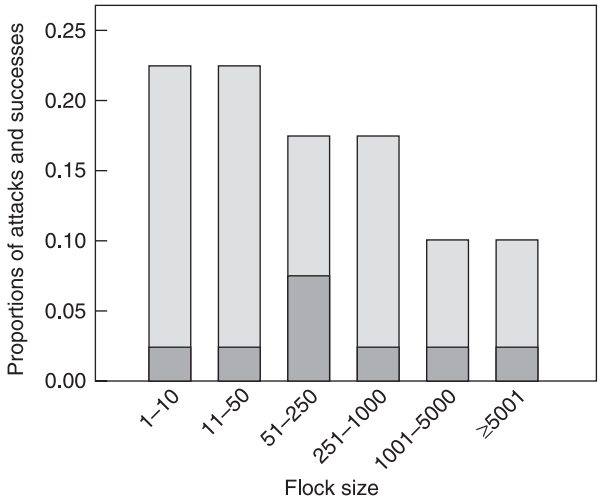

Figure 3. Flock size categories as targeted by falcons based on attacks for which the size of the targeted flock was recorded ($n = 40$). Smaller flocks are attacked more often than larger ones. Attack success, which is represented by the darker areas of shading, and only includes the attacks for which the flock size targeted was recorded, shows no correspondence with group size.

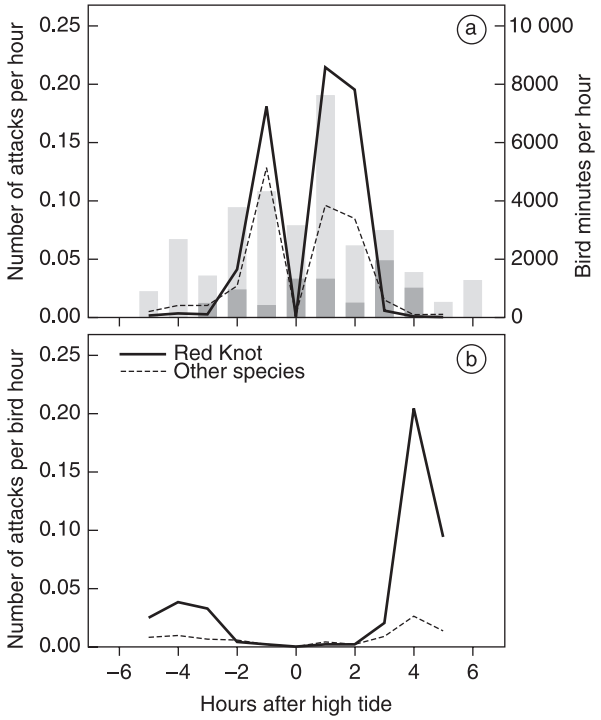

Figure 4. (a) Hunting pattern over the tidal cycle (shown by bars, darker shading representing successes) with reference to abundance of foraging birds, based on bird minutes per hour as observed in a quadrant in December 2006: Red Knot is represented by the solid line, other species (dashed line) are lumped for ease of viewing. (b) Hunting pattern over the tidal cycle expressed as the number of attacks per bird hours: Red Knot is represented by the solid line, other species (dashed line) are lumped for ease of viewing. All data are controlled for observation effort.

whereas for the larger female this amount varied from 13 to 15% of body mass (Ratcliffe 1993). As food requirements are expected to be lower in the semi-tropical conditions of the Banc d'Arguin (Wiersma & Piersma 1994), and taking into account that the female requirement per unit body mass is somewhat smaller than the requirements of the male due to her overall large body size (Ratcliffe 1993), we adjusted requirements assuming a daily food intake at the lower end of the range, i.e. 12% of body mass for males and 13% for females.

RESULTS

Most of the predators present were falcons (Lanner, Barbary and Peregrine), with at least four to five individuals in most years (Table 1). A few other avian predators were present (Kestrels *Falco tinnunculus*, Marsh C*ircus aeruginosus* and Montagu Harriers C. *pygargus*, and Short-eared Owls *Asio flammea*), which occasionally disturbed but rarely attacked shorebirds during our observations.

We observed an average of 8.9 attacks per day with an attack success of 28% (17 successes resulting from 61 attacks). Based on a normal distribution in Red Knot flock sizes (see Fig. 5) we distinguished five flock size categories, and found that small (1–10) to moderate-sized (11–50) flocks tended to be attacked more often (Fig. 3). Although no differences were detected in attack successes among flock sizes attacked (Fig. 3), in a smaller flock the individual risk to be killed in an attack was obviously higher. The majority of attacks (40 out of 77) were by surprise, 28 attacks were carried out openly and on eight occasions falcons stooped from great height. Co-operative hunting was observed only once by Barbary Falcons. Prey remains contained 91% shorebirds, 7.5% terns and gulls, and 1.6% passerines.

Raptor hunting increased towards high tide, when large numbers of shorebirds were forced to use the nearshore mudflats of Ebelk Aiznay and Baie d'Aouatif (Fig. 4a). Nevertheless, as nearshore foraging occurred in large flocks, in this time window the number of attacks per bird hour was fewer, and was particularly evident for the Red Knot (Fig. 4b). In fact, throughout

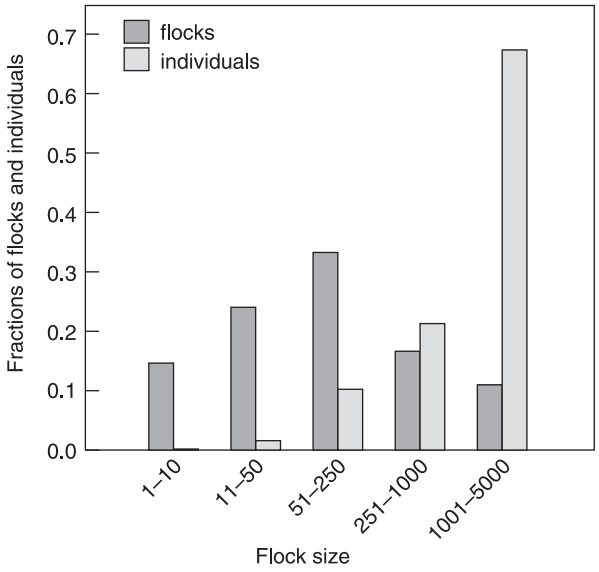

Figure 5. Frequency distribution of the size of Red Knot flocks encountered at Ebelk Aiznay in December 2006. Both the fractions of flocks (n = 380) and the fractions of individuals (n = 172 872) experiencing each flock size category are shown.

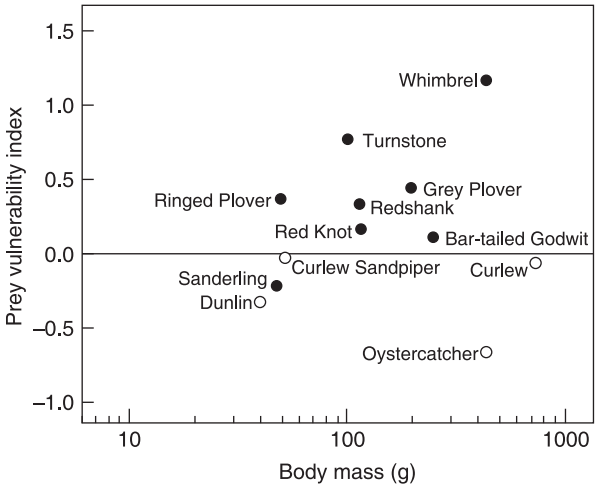

Figure 6. Prey vulnerability index as a function of body mass. Bird species are distinguished according to their relative tendency to forage near shorelines (closed dots = close, open dots = far). Little Stint *Calidris minuta* was excluded from this analysis because, due to its small size, high tide counts were not reliable. A $\log_{10}$ scale was applied to the x-axis. The prey vulnerability index values are given in Table 2.

the tidal cycle, the vast majority of Red Knots chose to forage with many flock mates (Fig. 5).

Whimbrel *Numenius phaeopus*, Ruddy Turnstone *Arenaria interpres*, Grey Plover *Pluvialis squatarola* and Ringed Plover *Charadrius hiaticula* experienced the highest mortality (approximately 2% or more of the local population were killed in the wintering area; in Whimbrel nearly 7% were killed), followed by Bar-tailed Godwit, Redshank *Tringa totanus* and Red Knot (slightly over 1%). The estimated direct mortality of Oystercatcher *Haematopus ostralegus*, Curlew Sandpiper *Calidris ferruginea*, Sanderling *Calidris alba* and Dunlin was minor (less than 1% of the local population, Table 2).

Dunlin (20 000), Red Knot (12 000) and Bar-tailed Godwit (7500) were by far the most abundant species (Table 2). Nevertheless, shorebird species were not killed according to their numerical abundance (χ^2_{12} = 470, $P < 0.001$). Prey vulnerability indices show that Bar-tailed Godwit, Ringed Plover, Ruddy Turnstone, Grey Plover, Redshank, Whimbrel and Red Knot were depredated more than expected from their abundance (Table 2). These species also commonly fed alone or in small flocks close to the dune-bordered shoreline (Fig. 6), including at high tide when most other birds were roosting. In Red Knot, such birds were mostly (92%) juveniles, as adult birds avoided nearshore mudflats unless the tide made outer mudflats unavailable (P.J. van den Hout unpubl. data). Vulnerability cannot be explained by body mass, but seems related to habitat selection (Fig. 6). This is most apparent in two similarly sized species: Whimbrel and Oystercatcher. The former, feeding solitary and close to the shoreline, was seven times more vulnerable than the more gregarious and shore-avoiding Oystercatcher.

For Dunlin, Red Knot and Bar-tailed Godwit the collected prey remains were sufficient to compare relative mortality by predation between juveniles and adults. Based on their relative abundance, Dunlin juveniles were killed 3.5 times more frequently than adults ($n_{\text{remains}} = 66, n_{\text{catch}} = 1616, \chi^2_1 = 35.5, P < 0.001$). In Red Knots this ratio was 5.4 ($n_{\text{remains}} = 103$, $n_{\text{catch}} = 991$, $\chi^2_1 = 199.7, P < 0.001$) and in Bar-tailed Godwit the ratio was 2.3 ($n_{\text{remains}} = 62$, $n_{\text{catch}} = 173$, $\chi^2_1 = 36.4$, $P < 0.001$; Fig. 7).

Annual survival in Red Knots was 88.9% for adults and 83.5% for juveniles (Table 3). Of the Red Knot population in our study area, 1.1% were estimated to be killed by large falcons (Table 2); 92% of these kills were juveniles. Thus, of the annual mortality of 11.1% for adult and 16.5% for juvenile Red Knots, 0.8 and 6.2%, respectively, can be explained by direct mortality due to predation in the wintering area.

Table 2. Predation pressure during winter by large falcons on shorebirds at the Iwik peninsula, Banc d'Arguin, Mauritania.

Species	*n*	Percentage in remains	Average high tide count (se)	Prey vulnerability index	No. taken per month	Percentage of population taken in 7 months
Curlew	1	0.2	139 (41)	–0.07	0.1	0.7
Whimbrel	18	3.6	274 (81)	1.17	2.6	6.7
Oystercatcher	1	0.2	925 (17)	–0.67	0.1	0.1
Bar-tailed Godwit	95	18.7	7 447 (43)	0.11	13.9	1.3
Grey Plover	13	2.6	641 (192)	0.44	1.9	2.1
Red Knot	133	26.2	12 166 (171)	0.16	19.4	1.1
Redshank	12	2.4	969 (488)	0.33	1.8	1.3
Ruddy Turnstone	27	5.3	1 171 (268)	0.76	3.9	2.4
Curlew Sandpiper	7	1.4	1 687 (469)	–0.03	1.0	0.4
Ringed Plover	32	6.3	1 726 (103)	0.36	4.7	1.9
Sanderling	4	0.8	1 676 (223)	–0.22	0.6	0.2
Dunlin	110	21.7	20 004 (7737)	–0.33	16.1	0.6
Little Stint	8	1.6	–	–	1.2	–
Terns and gulls	38	7.5	–	–	5.5	–
Passerines	8	1.6	–		1.2	–

The second column (*n*) shows absolute numbers per species of raptor prey remains found in 2002–06. The third column expresses these numbers as percentages of total remains. Average high tide counts over 2004–06 (± 1se) are shown in the fourth column. The number taken by raptors per month (sixth column) was calculated by multiplying the estimated average number of hunts per day (8.9) by success rate (0.28), and the percentage of that species in the raptor remains. To get an impression of predation mortality during the wintering period (which is around 7 months for most species) as a percentage of the population of a species, we assumed a constant predation pressure over all these months (last column). The shorebird species in this table are sorted by decreasing body mass. Terns and gulls, and passerines were lumped for ease of survey. Due to unreliable high tide counts for Little Stint *Calidris minuta*, some calculations were not performed for this species. Prey vulnerability indices are shown in the fifth column (see text and Fig. 6).

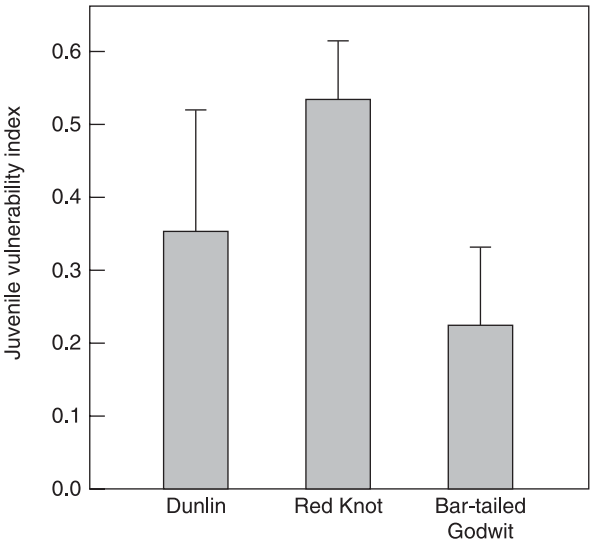

Figure 7. Prey vulnerability indices for juveniles, calculated separately for Dunlin, Red Knot and Bar-tailed Godwit. A value of zero would mean that an age-class of a particular species was killed exactly as expected by its relative abundance. The variance around the mean is depicted by error bars (± 1se).

Table 3. Results from survival analyses in MARK, including a correction for overdispersion $\hat{c}$ of 2.127.

			95% confidence interval	
Parameter	Estimate	se	Lower	Higher
Φ_1	0.835	0.068	0.657	0.930
Φ_2	0.781	0.040	0.692	0.850
Φ_3	0.889	0.037	0.794	0.944
P_{2003}	0.328	0.052	0.236	0.436
P_{2004}	0.515	0.043	0.429	0.599
P_{2005}	0.484	0.041	0.405	0.563
P_{2006}	0.674	0.053	0.565	0.768

Φ values refer to average annual survival of Red Knots: Φ_1 of juveniles in their first year after ringing, Φ_2 of adults in their first year after ringing and 'juveniles' in their second year after ringing, Φ_3 of adults two and more years after the year of ringing and 'juveniles' three and more years after the year of ringing. Φ_1 and Φ_3 were used as estimates for juvenile and adult survival, respectively. *P* is the resighting probability in a particular year.

Table 4. A review of published estimates of attack success by large falcons hunting on wintering shorebirds.

Location	Surface area (km^2)	Falcon species	*n*	Percentage success	Source
Banc d'Arguin, Mauritania	500	Lanner, Barbary, Peregrine	113	30	This study
Banc d'Arguin, Mauritania	500	Lanner, Barbary, Peregrine	32	22	Bijlsma (1990)
Boundary Bay, Canada	64	Peregrine	652	14*	Dekker and Ydenberg (2004)
Tyninghame, UK	5.5	Peregrine	233	11	Cresswell (1996)
Alberta, Canada	30	Peregrine	647	8	Dekker (1988)
Alberta, Canada	30	Peregrine	674	8	Dekker (1980)
Falsterbo and elsewhere in Sweden	N/A	Peregrine	260	7	Rudebeck (1950–51)
Tyninghame, UK	5.5	Peregrine	368	7	Cresswell and Whitfield (1994)

*Success rates differed per zone: (1) ocean shore–saltmarsh (44%), (2) the zone extending 0.5 km beyond zone 1 (11%); the zone 0.5 km beyond the saltmarsh (10%).

DISCUSSION

The key findings in this study are that: (1) shorebird species were not hunted relative to their abundance at the site, (2) juveniles were clearly overrepresented in raptor kills and (3) direct mortality due to predation accounted for only a small proportion of the annual mortality in the best studied shorebird, Red Knot.

Our observations that three large falcon species were the main predators of shorebirds on the Banc d'Arguin corroborates the study by Bijlsma (1990) on the Iwik peninsula in October 1988. Our calculations of mortality rates due to predation appear closely to cover food requirements of the raptors present. We observed a total bird mass taken per day of 340 g, a close fit to an estimated requirement of 315–483 g, reflecting situations of four (as in 2002, 2004, 2006) or five falcons (as in 2005) present in the area (see Table 1).

Attack success by large falcons as reported from several study sites varies considerably, and both Bijlsma (1990) and our study reported remarkably high values of attack success on the Banc d'Arguin (Table 4). As raptors preferentially target prey that are easy to catch (Bijlsma 1990, Cresswell & Quinn 2004), we speculate that this high attack success was simply due to the large population of wintering shorebirds always containing vulnerable individuals.

As opposed to large differences in mortalities between age-classes, per-capita mortality of wintering shorebirds on the Banc d'Arguin due to predation by large falcons was low, accounting only for 0.8% of the annual mortality of adult Red Knots and 6.2% of the annual mortality of juvenile Red Knots. These direct mortality levels are in contrast to studies from the northern temperate zone where predators were observed to kill up to half of the wintering population of shorebirds (Page & Whitacre 1975, Whitfield 1985, Cresswell & Whitfield 1994). Studies of predation may have focused on small and relatively high-risk coastal sites where predation is easy to observe (for an exception see Piersma *et al.* 1993). Two factors may together contribute to this danger, namely distance from cover and flock size (e.g. Quinn & Cresswell 2004). At sites where cover impedes an unobstructed view of the horizon, shorebirds are vulnerable to surprise attacks by predators (Piersma *et al.* 1993, Rogers *et al.* 2006). Foragers with few flock-mates may be at particular risk (Page & Whitacre 1975, Buchanan *et al.* 1988, Cresswell 1994a), because they lack the benefits of flocking, such as increased anti-predator vigilance, diluted risk when attacked and the opportunity to confuse predators in co-ordinated escape flight manoeuvres (Barnard & Thompson 1985, Krause & Ruxton 2002, Caro 2005).

Quite contrary to the Banc d'Arguin, certain saltmarshes or intertidal flats in small estuaries in the UK (Whitfield *et al.* 1988, Cresswell & Whitfield 1994, Cresswell 1996, Whitfield 2003a, 2003b), the USA (Page & Whitacre 1975) and western Canada (Dekker 1998) demonstrate the above-mentioned risk factors. These estuaries are surrounded by trees, bushes or other topographical structures, which allow stealth attacks: for instance by Sparrowhawks *Accipiter nisus* (in the UK) and Merlins *Falco columbarius* (in the USA and Canada). Correspondingly high mortality rates, biased towards nearshore foragers, were reported from these estuaries (Page & Whitacre 1975, Whitfield

1985, Cresswell & Whitfield 1994). In the Scottish estuary of Tyninghame, Redshanks were 10 times more vulnerable than the shore-avoiding and highly gregarious Red Knot (30–60% against 3–4% of the respective populations were killed in three winter periods, Cresswell & Whitfield 1994), and the same ratio was found in an earlier study on the rocky shore of Scoughal and the estuary of Tyninghame (Whitfield *et al.* 1988). Bolinas Lagoon, California, offers another example of a small sheltered estuary where relatively large numbers of shorebirds were killed (Page & Whitacre 1975, Kus *et al.* 1984). Such high percentages of mortality in a wintering population may be explained by the fact that compared with the Banc d'Arguin, relatively few shorebirds stage in these areas, which may result in a ratio of one raptor to a few hundred or a few thousand shorebirds. On the Banc d'Arguin this ratio is about one raptor to at least 10 000 shorebirds. This low ratio compared with the temperate situation may be explained by the fact that habitat suitability for shorebirds and falcons is governed by different dimensions. Shorebird abundance is limited by the surface area of suitable mudflat, whereas the raptors can never benefit to the full extent from increases in shorebird abundance because for their attacks to be effective they are limited by the linear dimensions of coastline available. That the Banc d'Arguin may already be largely occupied by resident Lanner and Barbary Falcons may explain why the majority of migrating Peregrines appear to skip the Banc d'Arguin as a winter feeding area (Bijlsma 1990, Table 1). The open character of the Banc d'Arguin allows shorebirds to avoid surprise attacks by feeding far from cover as long as the tide permits. Yet, some classes of individuals appear to accept higher levels of predation risk by foraging close to cover, and in smaller flocks, even at low tides. This may be due to species-specific foraging characteristics or habitat segregation among age-classes.

First, some species as a rule often find their food alone or in small flocks, close to the shoreline (Fig. 6). For example, Whimbrels are solitary feeders, feeding exclusively on crabs, most of which are Fiddler Crabs *Uca tangeri*, that have a nearshore distribution (Altenburg *et al.* 1982, Zwarts 1990, Zwarts & Blomert 1990, Zwarts & Dirksen 1990). Likewise, Ruddy Turnstones feed in dead seagrass washed ashore, a habit also found by Redshanks and Bar-tailed Godwits, particularly at high tide when mudflats become unavailable. The vulnerability of Ringed and Grey Plovers may not only have been caused by their solitary (territorial) feeding habit (Altenburg *et al.* 1982), but also by the fact that both species stay on sandy shores and on barren sand throughout the tidal cycle, thus creating a large time window for attacks (see also Altenburg *et al.* 1982). Remarkably, Sanderlings, which often feed together with Ruddy Turnstones, and rest together with Ringed Plovers on the barren sand (Altenburg *et al.* 1982, P.J. van den Hout, B. Spaans & T. Piersma pers. obs.), nevertheless seemed not particularly vulnerable (Fig. 6).

Secondly, within a species, age-classes may differ in their trade-off between food and danger. Red Knot is a prime example of a species that limits nearshore foraging to times when farshore mudflats are unavailable due to high tide (Piersma *et al.* 1993). Although in our study these shorebird aggregations attracted predators (Fig. 4a), encounters per bird hour were fewer, demonstrating the benefit of visiting these nearshore foraging sites in large numbers (Fig. 4b). This anti-predator advantage is consistent with the observation that in general the vast majority of Red Knots avoided foraging in small flocks (Fig. 5). Yet, small numbers of juvenile Red Knots did not follow this pattern of predator avoidance, and foraged and rested in nearshore groups of at most a few tens of birds throughout the tidal cycle (P.J. van den Hout unpubl. data). Similar observations were reported by Van der Have *et al.* (1984) for Dunlin in the Wadden Sea of the Netherlands, in autumn, where the juveniles staged in smaller groups close to the mainland shores. Age-related mortalities in Dunlin in a similar context have been reported by Kus *et al.* (1984).

But why would some juvenile Red Knots take these risks? We suggest that competition (see Goss-Custard 1980, Van Gils *et al.* 2004, Van Gils & Piersma 2004, Vahl *et al.* 2005), the currency used to evaluate foraging decisions (Stephens & Krebs 1986) and experience may relegate juvenile individuals to dangerous sites (P.J. van den Hout unpubl. data). Cresswell (1994b) observed this in Redshanks in Tyninghame, Scotland. Here, juveniles were excluded from the farshore mussel beds by adults, forcing the former to forage on the saltmarsh where they were nearly five times more likely to be killed by Sparrowhawks. Yet, as energy intake rates on the saltmarsh were higher, adults seemed to consider minimizing predation risk, rather than maximizing intake rate. At least for Red Knot we may have witnessed a similar phenomenon on the Banc d'Arguin. Here, adult birds may exclude juvenile conspecifics from farshore and thus safer foraging areas, causing them to feed along the more risky shoreline habitat (P.J. van den Hout unpubl. data).

In conclusion, the low mortality rates that we observed on the Banc d'Arguin cannot be used as evidence against the potential importance of predators in shorebird ecology (Lind & Cresswell 2005, Ydenberg *et al.* 2007). Instead, they may reflect the ability of the majority of shorebirds to effectively avoid predation. The relative differences in mortality rates between classes of individuals indicate that non-lethal effects of predation, including enhanced risk of starvation (McNamara & Houston 1994, Houston & McNamara 1999), are probably much more important in moulding patterns of migration and other life-history decisions. At the same time, they demonstrate a strong selection for behaviours such as predator avoidance, foraging strategies and competitive foraging abilities that allow animals to compensate for direct predation risk.

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